

PREDATOR-PREY RELATIONSHIPS AND REPRODUCTION OF THE BARN OWL IN SOUTHERN TEXAS¹

LEE C. OTTENI, ERIC G. BOLEN, AND CLARENCE COTTAM

THIS study was designed to reveal the ecological interactions existing between the food habits and breeding of Barn Owls (*Tyto alba*) in southern Texas. Specific areas of investigation included determination of (a) Barn Owl food habits, (b) relative abundance of prey populations, and (c) Barn Owl nesting biology. Certain portions of the study began in 1965, whereas intensive field work was initiated and continued in 1969 through 1971.

STUDY AREA

Field work was conducted on the Rob and Bessie Welder Wildlife Foundation (hereafter referred to as the Welder Refuge), eight miles northeast of Sinton, San Patricio County, Texas. The Welder Refuge covers 7,800 acres of a broad ecotone between the Coastal Prairies and Rio Grande Brushlands. The region supports a complex biota of nearly 1,400 flowering plants and more than 500 animal species. A subhumid climate prevails; hot summers and mild, short winters are characteristic together with frequent late summer and fall hurricanes. Rainfall averages about 31 inches per year, but the fluctuation between years is highly variable with the extremes, rather than the average, influencing the permanent vegetation.

Box and Chamrad (1966) described the soils and plant communities of the area. The vegetation can be generally considered a brush-grass complex developing on (a) clay and clay loam sites, (b) sandy and sandy loam sites, (c) bottomland sites, and (d) semi-permanent lake sites. Our work centered on eight of the major plant communities present at the Welder Refuge.

METHODS

Capture and handling of owls.—Most adult Barn Owls were caught in nest boxes erected throughout the Welder Refuge. Snares set on top of the nest boxes were also used if the resident owl could not be captured inside the box. Nesting owls were returned to the box and detained for several minutes by blocking the entrance hole. This usually was sufficient to calm the bird and inhibit its flushing.

Adult owls were banded with standard aluminum leg bands. Juveniles of sufficient size were also banded. The sex of adults were determined only during the breeding season by cloacal examination. The female Barn Owl develops an incubation patch and, if still in the laying period, also has an enlarged, reddened vent. No reliable method was otherwise found to determine the sex of either adult or immature owls.

Periodic inspection of the nest boxes yielded information on clutch size, nesting success, breeding chronology, and general nesting behavior.

Analysis of owl foods.—Barn Owl foods were determined from an examination of pellets collected on a monthly basis from nest boxes and roost sites. The analysis included the

¹ Contribution No. 151, Rob and Bessie Welder Wildlife Foundation, Sinton, Texas.

frequency (percentage) and the minimum number of prey items in the pellets. Prey species were identified by comparison with museum specimens and by the mammalian skull key developed by Glass (1951). Bones from birds were compared with specimens at the U.S. National Museum.

Prey census.—Small mammal populations were estimated in eight of the major plant communities described in part by Box and Chamrad (1966): Bunchgrass-Annual Forb; Mesquite-Buffalograss; Chaparral-Bristlegrass; Pricklypear-Shortgrass; Paspalum-Aquatic Weed; Live Oak-Chaparral; Annual Forb Disclimax (i.e. disturbed sites); Texas Wintergrass Stands.

Trapping stations at 25-foot intervals formed a grid of eight by six trap lines. Trapping periods consisted of 48 traps checked for three consecutive nights. Sex, age, species, and trapping station were recorded for each captured mammal which was ear-tagged and released at the point of capture. The composition and relative abundance of each population were determined using the marking-and-recapture method (Davis, 1959). Details of the habitat preferences and other ecological aspects of the small mammal populations not directly relevant to the present study are as yet unpublished.

The blackbird population, consisting of Red-winged Blackbirds (*Agelaius phoeniceus*), Boat-tailed Grackles (*Cassidix mexicanus*), Brown-headed Cowbirds (*Molothrus ater*), and Bronzed Cowbirds (*Tangavius aeneus*), was also estimated with the mark-and-release method. Large (5 × 16 × 18 feet) poultry-wire decoy traps containing live decoy birds, food, and water were used to capture blackbirds.

RESULTS

Dynamics and composition of prey populations.—No attempt was made to fully estimate the rodent densities on the Refuge because of non-random sampling bias inherent in the trapping procedure (cf. Krebs, 1966). Instead, the objective was to measure trends important to the availability of prey to Barn Owl predation. Trap success provided an adequate measure for these fluctuations (Table 1).

Rodent populations declined from the summer of 1969 to the following winter and spring of 1970 (Table 1). The lowest level of trapping success was reached in May 1970, and thereafter it increased to 48 per cent success in the fall of 1970. This peak was again followed by a period of decline that stabilized during the winter and spring of 1971.

In 1969, prior to live trapping, small mammals were snap-trapped in the major plant communities to gain a cursory view of the composition of the rodent population. The results showed the highest percentage of rats found during the duration of the study (Table 2). Following the summer of 1969, the rat population declined to less than 1 per cent of the catch.

Mice dominated the catch throughout the study; they varied from 73 to 99 per cent of the overall rodent population. These data indicate that the decline in the rodent population was strongly influenced by a disproportionate reduction in the rat populations that was not accompanied by marked losses of mice.

TABLE 1
FLUCTUATIONS IN RODENT POPULATIONS AS SHOWN BY TRAP SUCCESS, WELDER WILDLIFE
REFUGE, 1969-1971

Date	Number		Percentage trap success
	Traps set	Traps entered	
July, 1969	540	154	28.5
January, 1970	288	37	12.8
February, 1970	192	24	12.5
March, 1970	288	57	19.8
April, 1970	288	26	9.0
May, 1970	864	17	1.9
June, 1970	2,160	83	3.8
July, 1970	1,296	84	6.5
August, 1970	2,160	178	8.2
November, 1970	288	139	48.3
January, 1971	2,160	388	19.3
February, 1971	432	83	19.2
March, 1971	1,584	351	22.2
May, 1971	1,584	299	18.9
Total	14,124	1,920	$\bar{x} = 13.6$

Blackbird populations.—Our estimates indicate that about 50,000 resident and migratory blackbirds roosted each winter in sites dominated by round-stem rushes (*Scirpus californicus*). The spring and summer population was estimated at 15,000 birds. The population included Red-winged Blackbirds and lesser proportions of cowbirds and grackles.

An attempt to measure the rate at which Barn Owls preyed on the blackbird population employed the methods of Southern (1955). Birds were trapped, banded, and released, and although 2,413 blackbirds were marked, no bands were subsequently recovered from the owl pellets. Thus it was not possible to directly assess the proportion of blackbirds taken as prey by the owls. However, as noted above, the availability of blackbirds was never limited.

Bias in Barn Owl food habits studies.—Barn Owls as well as many other species of raptors, regurgitate pellets of bone, feathers, and fur. These form in response to the mechanical barrier posed by a small pyloric opening (Reed and Reed, 1928); the materials are ejected in virtually an undigested mass because of the absence of free acidity in the owl stomach. Hence, examination of the pellets generally provides a reliable technique for determination of owl food habits. However, at least two sources of error may occur. First, there is the potential failure to collect one of the two pellets usually formed in each 24-hour period. A small pellet is formed and regurgitated during the night

TABLE 2

PERCENTAGE COMPOSITION OF LIVE- AND SNAP-TRAPPED SMALL MAMMALS, WELDER WILD-LIFE REFUGE, 1969-1971

Species	1969	1970				1971		Total individuals
	Summer	Winter	Spring	Summer	Fall	Winter	Spring	
Pigmy Mouse	72.7	89.9	82.5	85.1	94.9	82.6	91.6	1,749
Harvest Mouse	4.1	9.3	4.8	3.8	1.4	14.9	6.4	184
Deer Mouse	1.0	—	6.3	3.4	—	1.5	1.0	15
Hispid Pocket Mouse	—	—	—	0.7	—	—	—	2
House Mouse	—	—	0.8	—	—	0.1	0.3	3
Sub-total	77.8	99.2	94.4	93.0	96.3	99.1	99.3	1,953
Wood Rat	9.6	—	0.8	0.4	—	—	—	30
Rice Rat	8.3	—	1.6	0.4	1.4	—	—	29
Cotton Rat	—	0.8	2.4	2.7	—	0.1	0.3	12
Sub-total	17.9	0.8	4.8	3.5	1.4	0.1	0.3	71
Least Shrew	4.1	—	0.8	3.4	2.2	0.6	0.7	32
Total Individuals	290	118	126	262	139	822	299	2,056

while the birds are still foraging whereas a second and larger pellet is deposited at the diurnal roost (Guerin, *in* Wallace, 1948:25). In our study, the nesting boxes were the sites of diurnal roosting so that we were able to collect and examine only these pellets and not those scattered elsewhere. Secondly, errors may occur when soft-bodied foods (invertebrates, nestling birds, etc.) were eaten (Glading et al., 1943). These foods may be overlooked or not accurately identified. Errington (1932) noted that the foods of very young owlets may be masked because of their temporary proficiency at digesting calcium and thus dissolving many of the bones otherwise diagnostic of their food habits.

Year-to-year variation in Barn Owl foods.—Variations in fundamental predator-prey interactions due to environmental factors often complicate a full understanding of Barn Owl food habits. Physical changes in the habitat (floods, rainfall, etc.) as well as biological changes have much to do with the pressure exerted on prey populations (Craighead and Craighead, 1956: 147). However, we are able to evaluate the Barn Owl diet in southern Texas over a seven year period, 1965-1971, inclusive, using the pellet analysis technique. This method permits us to determine the frequency of each prey's occurrence in the diet, but not directly, determination of either volume or availability.

Mice represented 4,715 or 40 per cent of the 11,625 items identified as owl foods. The species included pigmy mice (*Baiomys taylori*), fulvous

TABLE 3
PERCENTAGE FREQUENCY FOR BARN OWL FOODS ON THE WELDER WILDLIFE REFUGE,
1965-1971

Species	1965	1966	1967	1968	1969	1970	1971
Mammals							
White-footed Mice	1.3	1.8	1.5	3.5	2.0	2.2	0.6
Pigmy Mice	27.5	23.7	8.6	2.6	14.8	30.0	20.0
Fulvous Harvest Mice	12.9	30.9	5.7	2.0	2.5	2.0	5.1
Pocket Mice	31.1	5.2	3.3	0.5	1.8	1.2	—
Mice Sub-total	72.8	61.6	19.1	8.6	21.1	35.4	26.7
Cotton Rat	2.3	14.0	20.8	9.2	12.9	11.1	2.0
Rice Rat	1.1	1.2	2.2	5.7	17.7	7.1	5.4
Wood Rat	—	1.1	12.1	25.9	1.6	0.7	—
Rat Sub-total	3.4	16.3	35.1	40.8	32.2	18.9	7.4
Least Shrew	10.0	11.9	9.8	9.0	24.5	24.0	34.0
Cottontail	1.4	4.4	7.6	4.3	0.1	0.7	0.4
Pocket Gopher	7.1	2.7	8.7	2.4	0.5	0.4	0.8
Unidentified	4.2	—	0.2	0.4	1.7	—	—
Mammal Sub-total	98.9	96.9	81.4	65.5	80.1	79.6	69.3
Birds—Roosting							
Over Water	—	1.0	13.7	17.2	13.4	16.4	17.0
Over Land	1.1	1.6	4.4	17.1	3.2	1.3	3.3
Bird Sub-total	1.1	2.6	18.1	34.3	16.6	17.7	20.3
Insects							
Grasshopper	—	0.3	1.0	—	2.6	2.6	10.4

harvest mice (*Reithrodontomys fulvescens*), white-footed mice (*Peromyscus leucopus*), and hispid pocket mice (*Perognathus hispidus*). Of these, all but white-footed mice were subject to pronounced fluctuations in the owl diet during the seven year period (Table 3). A crash in the mouse populations was particularly noticeable in 1968, following the earlier (October 1967) inundation by Hurricane Beulah.

Gray wood rats (*Neotoma micropus*), rice rats (*Oryzomys palustris*), and cotton rats (*Sigmodon hispidus*) represented 21 per cent (2,430 individuals) of the diet. Gray wood rats were not present in the pellets in 1965, nor were they important in 1966. Their numbers began to increase in 1967 (12 per cent of the diet), and in the year following the hurricane, they were a major food item (26 per cent). The principal habitat of the wood rat, clay soil

communities, was not flooded by Hurricane Beulah. Rice rats were particularly evident only in 1969.

Least shrews (*Cryptotis parva*) were a relatively stable food throughout the study. Overall, the pellets contained 1,861 individuals (16 per cent) and varied from 9 to 34 per cent in annual occurrence. Pocket gophers (*Geomys bursarius*) comprised 4 per cent (458 individuals) of the total diet. Cottontail rabbits (*Sylvilagus floridanus*) made up 318 separate items or 3 per cent of the diet. Adult rabbits are likely less vulnerable as Barn Owl prey because of their comparatively large size; all of the rabbit skulls taken from the pellets between 1969 and 1971 were from sub-adults, and it is probable that Barn Owls select only the smaller, and thus younger rabbits as food.

Birds roosting in association with aquatic communities at the Welder Refuge occurred 1,066 times (9 per cent) in the owl pellets. These were primarily members of the Icteridae: 182 grackles, 390 Brown-headed Cowbirds, and 435 Red-winged Blackbirds. The Barn Owls apparently used the abundant icterid populations as a buffer group when the availability of rodents was low (Table 3). With the decline of mice in 1967, icterids in pellets increased from less than 1 per cent in 1966 to 14 per cent in 1967. Further declines in the rodent population in 1970 and 1971, indicated in both the live trapping census and in the pellet analysis, were again compensated by increased use of blackbirds as food.

Other birds contributed 403 individuals (3 per cent) to the owl diet. Non-passerine species included Sparrow Hawks (*Falco sparverius*), Mourning Doves (*Zenaidura macroura*), Inca Doves (*Scardafella inca*), Yellow-billed Cuckoos (*Coccyzus americanus*), and 81 Bobwhite (*Colinus virginianus*). An additional 308 individual passerine birds were identified; these were primarily 111 Dickcissels (*Spiza americana*) and lesser numbers of 28 other species. The occurrence of Bobwhite and other landbirds in the Barn Owl diet was prominent only in 1968.

Grasshoppers of the family Acrididae were infrequently found in the pellets although, in 1971, 10 per cent of the pellets contained grasshopper remains. Other invertebrates were of even rarer occurrence.

Seasonal variation.—The seasonal food-habits picture is least representative in late summer and early fall, when few pellets were collected. At this time, young Barn Owls were awing and expanding their range, and the adult birds used established roosts less than before.

There were pronounced seasonal changes in the percentage of prey species. Predation on birds, predominantly those that roost over water, was characterized by a seasonal variation. In the winter, predation on birds was directed toward adult migratory blackbirds, whereas in late spring and early summer predation on nestlings increased. Likewise, there was an inverse relationship

TABLE 4
SEASONAL VARIATION IN BARN OWL FOODS, WELDER WILDLIFE REFUGE, 1969-1971
Data are percentage frequency.

Species	1969		1970				1971	
	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring
Mammals								
Mice	42.2	62.3	47.8	5.9	2.7	16.6	24.7	27.9
Rats	7.2	2.2	10.6	22.5	30.5	13.7	7.1	8.6
Shrews	28.3	33.3	27.0	16.8	42.0	34.3	34.6	32.5
Birds Roosting Over								
Water	0.4	2.2	6.0	41.7	17.0	6.0	12.8	27.4
Land	0.8	—	—	1.5	3.0	9.8	3.8	2.0
Insects								
Grasshopper	21.1	—	1.9	0.8	—	14.7	15.7	—

in the proportion of rats versus mice. The greatest number of rats in the diet (summer, 1970) corresponded to the lowest number of mice. Conversely, the period when mice were consumed in great numbers (fall, 1969) coincided with a small amount of rat foods. These relationships, shown in Table 4, reflect opportunistic hunting by Barn Owls in various habitats as seasonally characterized by prey availability.

Biomass.—Pellet analysis alone provides only an index to the numbers of food items taken, but if the average weight of individual prey species can also be determined, an index of biomass can be developed. Biomass is ecologically significant because small species (pigmy mouse, etc.), while numerically abundant in the pellets, may provide relatively little bulk to the Barn Owl diet. Hence, using the weights of specimens collected in live traps, the mouse population which numerically contributed 41 per cent of the owl foods actually comprised only 11 per cent of the biomass (Table 5). In contrast, the rat population contributed 50 per cent of the biomass and, numerically, only 21 per cent of the diet.

Using the biomass estimates shown in Table 5, we found that a strong relationship exists between the percentage frequency of each class of food and the percentage biomass in the Barn Owl diet. Mammals comprised 85 per cent of the individual prey and 87 per cent of the biomass and birds, 13 per cent of the individuals and 13 per cent of the biomass.

Barn Owl breeding biology: nest sites.—The Barn Owl primarily nests in tree cavities, holes in river banks, and in crevices in cliffs although nests in towers, barns, and other buildings are common. At the Welder Refuge, Barn

TABLE 5

NUMERICAL AND BIOMASS COMPOSITION OF BARN OWL FOODS AS DETERMINED BY PELLET ANALYSIS, WELDER WILDLIFE REFUGE, 1965-1971

Species	Number individuals	Percentage of individuals	Estimated weight (grams)	Estimated biomass	Percentage of estimated weight
Mammals					
Pigmy mouse	2,252	19.7	9.5	21,394	2.9
White-footed mouse	208	1.8	20.5	4,264	0.6
Fulvous harvest mouse	1,161	10.2	10.5	12,190	1.6
Hispid pocket mouse	1,094	9.6	42.0	45,948	6.1
Cotton rat	1,232	10.8	170.0	209,440	28.0
Rice rat	660	5.8	56.0	36,960	5.0
Wood rat	538	4.7	236.0	126,968	17.0
Least shrew	1,861	16.3	4.5	8,374	1.1
Cottontail	318	2.7	250.0	79,500	10.6
Pocket gopher	458	4.0	229.0	106,256	14.2
Unknown mammals	166	1.4			
Sub-total	9,740	85.4		651,294	87.1
Birds					
Boat-tailed Grackle	182	1.6	120.0	21,840	3.0
Brown-headed Cowbird	390	3.4	40.0	15,600	2.1
Red-winged Blackbird	435	3.8	65.0	28,275	3.8
Dickcissel	111	1.0	150.0	16,650	2.2
Miscellaneous birds ^a	291	2.5	50.0	14,000	1.9
Unknown birds	69	0.6			
Sub-total	1,478	12.9		96,365	12.9
Insects					
Grasshoppers	190	1.7	2.0	380	0.1
All species	11,408	100.0		748,059	100.0

^a Birds each providing less than 1.0 per cent total biomass include a wide range of passerines and 81 individual Bobwhite (*Colinus virginianus*) and 38 Virginia Rails (*Rallus limicola*), among other non-passerine species.

Owls made extensive use of nesting boxes described elsewhere (Bolen, 1967). Of the 112 Barn Owl nests found in this study, 109 were located in 36 nesting boxes situated on the Welder Refuge; the additional three nests were located in a small shed also on the Refuge grounds.

Nest materials.—Pellets regurgitated in the confines of the nest boxes are subsequently trampled underfoot and in time become a thick, coarse mat of organic debris underlying the eggs. Wallace (1948) also reported that Barn

TABLE 6
MONTHS OF NEST INITIATION FOR BARN OWLS, WELDER WILDLIFE REFUGE, 1965-1971

Date	Number of nests							All years		
	1965	1966	1967	1968	1969	1970	1971 ^a	Number	Mean	Per cent
January	3	7	-	-	5	-	-	15	2.1	13.4
February	2	2	10	4	2	4	-	24	3.4	21.4
March	3	3	7	7	7	7	4	38	5.4	33.9
April	1	1	2	-	-	2	1	7	1.0	6.2
May	1	-	-	1	-	1	-	3	0.4	2.7
June	5	7	-	-	2	-	-	14	2.0	12.5
July	5	2	-	-	-	-	-	7	1.2	6.2
August	1	1	-	-	-	-	-	2	0.3	1.8
September	1	-	-	-	-	-	-	1	0.2	0.9
October	-	1	-	-	-	-	-	1	0.2	0.9
Total	22	24	19	12	16	14	5	112	—	100.0

^a Field study ended in June, 1971.

Owls crushed many of their pellets when nesting; no other materials are involved in nest construction.

Nesting chronology.—Nests were initiated four times in January, twice in February, and once in March (Table 6). These differences suggest that the onset of nesting may be regulated by the availability of food more so than by such environmental features as photoperiod or temperature.

The length of the Barn Owl nesting season in south Texas was determined from the beginning dates of each year's first and last nests. The last nests, respectively, were started in September of 1965, October of 1966, April of 1967, May of 1968, June of 1969, May of 1970, and April of 1971. The average nesting season lasted 5.3 months during the period 1965-1971. Nesting attempts increased rapidly as each season began and reached their peak in March (Table 6).

Number of broods per season.—At the Welder Refuge female Barn Owls usually produce only one brood per year. However, there was one instance (1965) of a banded Barn Owl raising two broods in the same calendar year. Male Barn Owls feed their mates while the latter incubates, whereas after hatching both parents tend the flightless young and remain with the brood for some time even after flight is attained. This pattern of events does not usually permit time for a second clutch during the nesting season unless the male were to divide his efforts between the re-nesting female and the owlets of the first nest.

Clutch size.—Of 112 separate clutches under study, 91 were considered as

TABLE 7
MEAN CLUTCH SIZE FOR 91 BARN OWL NESTS, WELDER WILDLIFE REFUGE, 1965-1971

Clutch size	No. clutches	Total eggs
3	19	57
4	12	48
5	29	145
6	24	144
7	4	28
8	3	24
Totals	91	446
Mean clutch size		4.9
Standard deviation		1.3

completed sets. The size of these varied from 3 to 8 eggs per nest with a mean clutch size of 4.9 eggs (Table 7). The additional 21 nests, 11 with 1 egg and 10 with 2 eggs, were excluded from the analysis as incomplete clutches.

Lack (1947) found a tendency for the mean clutch size of owls to increase with latitude and with an increased abundance of rodents. Henny (1969) reported a mean clutch size of 5.3 eggs for Barn Owls nesting in Switzerland (Lat. 46-47 N) and 4.9 eggs for those in Maryland (Lat. 38-43 N). Clutch sizes for the 68 Maryland nests and the 91 nests in this study (Lat. 28 N) thus yielded identical results. It thus appears that clutch sizes in Barn Owls are more closely associated with factors other than with latitude. Lack (1954: 22) also suggested that the number of eggs laid by each species (i.e. average

TABLE 8
NEST AND EGG SUCCESS FOR THE BARN OWL, WELDER WILDLIFE REFUGE, 1965-1971

Year	Nests			Eggs			
	Attempts No.	Hatched No.	Percentage successful	Layed No.	Hatched No.	Percentage successful	Clutch mean
1965	19	10	52.6	95	45	47.3	5.0
1966	21	12	57.1	106	57	54.2	5.0
1967	16	13	81.2	86	60	69.7	5.4
1968	12	11	91.6	62	38	61.2	5.2
1969	14	11	78.6	63	35	55.5	4.5
1970	6	2	16.6	23	8	34.7	3.8
1971	3	1	33.3	11	2	18.1	3.7
Totals	91	60	65.9	446	245	54.9	4.9

TABLE 9
INFLUENCE OF PREY AVAILABILITY ON BARN OWL BREEDING SUCCESS, WELDER WILDLIFE
REFUGE, 1965-1971

Reproductive effort	Abundance of prey (scale 1-14) ^a	
	Abundant (3 years) 14-7	Scarce (4 years) 6-1
Number of pairs breeding	14.0	11.5 N.S.
Mean clutch size	5.0	4.4 N.S.
Young fledged/pair	2.5	1.0*

^a Abundance scale defined as biomass per year divided by total biomass for all years, rounded to nearest whole number.

* $P < 0.05$.

clutch size) has been established by natural selection to correspond with the largest number of young that can be successfully raised. Successful rearing, in turn, is based on the amount of food that is available and provided to the young by the adults. This hypothesis as it relates to the clutch size of the Barn Owls nesting in southern Texas, is discussed in a following section.

Nesting success.—Nesting success of the Barn Owls was 66 per cent for the seven year period of our study. Losses occurred because of abandonment (10 per cent), swarming bees (1 per cent), and disturbances associated with our periodic inspection of the nests during incubation (23 per cent). Of 446 eggs laid in these nests, 245 (55 per cent) later hatched. Year-by-year details are shown in Table 8.

Evaluation of prey biomass and Barn Owl reproduction.—Juvenile Barn Owls remain in the care of their parents for more than two months after fledging. Prey populations during this time must, therefore, be sufficient to provide food for the adults and the young. Food supplies are thus critical to Barn Owl reproductive success for about 18 weeks.

The ultimate measure of breeding success is the average number of young raised per pair (Lack 1966:142). Accordingly, we found that Barn Owls raised 1.5 times as many young per pair in years when prey was abundant than in years when prey populations were more limited (Table 9).

A statistical comparison between the biomass of mammals in the Barn Owl diet and the number of young owls raised per pair indicated that mammals were a dietary requirement for successful reproduction. Declines in the biomass of mammals were significantly correlated ($r = 0.913$) with a corresponding decline in the number of owlets fledged (Fig. 1). The otherwise abundant bird population alone did not sustain successful Barn Owl reproduction.

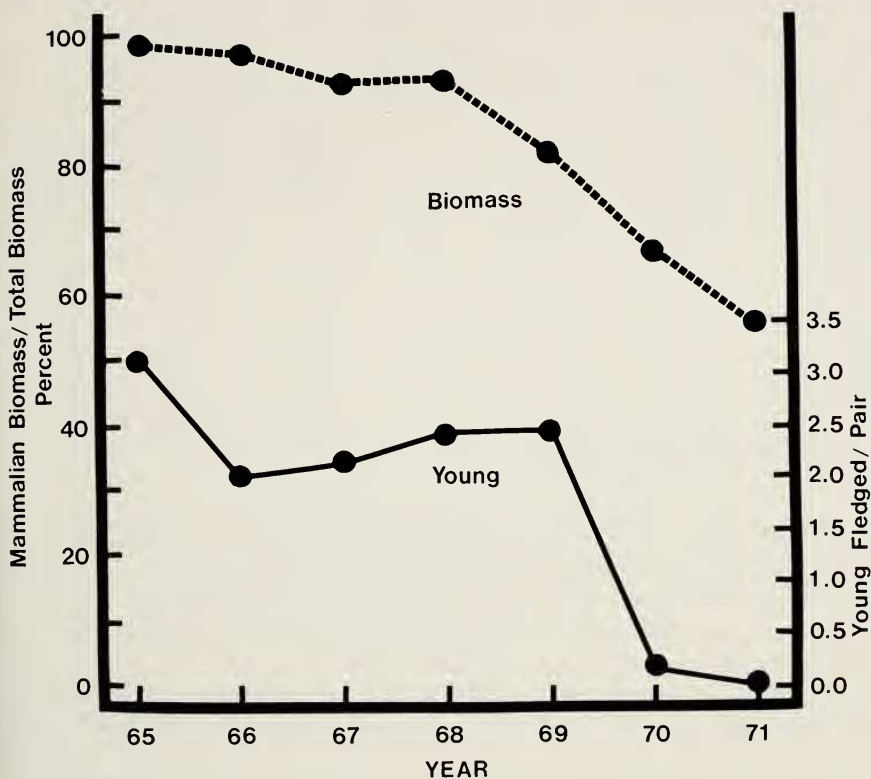


FIG. 1. Reproductive success of the Barn Owl relative to the percentage of mammalian biomass in the owl diet. Statistical correlation of these data was highly significant ($r = 0.91, P < 0.01$).

The Welder Refuge supported 12 to 17 breeding pairs of Barn Owls from 1965 through 1970. During this time, the pellet analysis indicated that the mammalian biomass was abundant through the breeding season of 1969. Thereafter, however, rodent numbers and their biomass rapidly declined in the winter of 1969-70. The 12 pairs of Barn Owls attempting to breed at this time experienced a marked reduction in the number of young fledged: fully 92 per cent more young were successfully raised in 1969 than in 1970 (Table 10).

The three owlets actually fledged in 1970 were indeed nourished by a diet of 91 per cent blackbirds. Two owlets of another nest—abandoned at 5 weeks of age—were fed a diet of 72 per cent blackbirds prior to the time of parental abandonment. The significant amount of birds in the diet of these owlets was further evidence that rodents were not available in the spring and summer

TABLE 10
BREEDING HISTORY OF BARN OWLS, WELDER WILDLIFE REFUGE, 1965-1971

Year	Breeding pairs	Mean clutch	Young fledged	Young fledged per pair	Abundance index of prey based on pellet analysis ^a	Biomass ratio of mammals to birds
1965	12	5.0	38	3.2	8	99- 1
1966	17	5.0	35	2.0	6	98- 2
1967	16	5.4	32	2.1	14	92- 8
1968	12	5.2	25	2.4	6	93- 7
1969	14	4.5	34	2.4	7	83-17
1970	12	3.8	3	0.2	4	67-32
1971	5	3.7	0	0.0	1	55-45

^a Abundance index defined as biomass per year divided by total biomass for all years, rounded to nearest whole number. The index reads from 14 (abundant) to 1 (scarce).

months of 1970. The amount of rodent biomass available to the Barn Owl population continued to decline after 1970 (Table 11).

In 1971, 58 per cent fewer pairs nested than in 1970 (five vs. 12 pair). This again indicated that the Barn Owl population had adjusted their reproductive efforts to the lower population level of rodents. The mean clutch size was slightly reduced whereas the number of completed clutches was 50 per cent lower than in 1970. The information from both the trapping and

TABLE 11
SEASONAL VARIATION IN BIOMASS AND NUMBERS OF LIVE-TRAPPED MAMMALS, WELDER WILDLIFE REFUGE, 1969-1971.

Species	1969		1970			1971		Total
	Summer	Winter	Spring	Summer	Fall	Winter	Spring	
Pigmy Mouse	2,004	1,007	988	2,118	1,254	3,059	703	11,133
Harvest Mouse	126	115	63	105	21	1,302	199	1,931
Deer Mouse	61	—	164	184	—	246	61	716
Hispid Pocket Mouse	—	—	—	84	—	—	—	84
House Mouse	—	—	10	—	—	10	10	30
Wood Rat	6,608	—	236	236	—	—	—	7,080
Rice Rat	1,344	—	112	56	112	—	—	1,624
Cotton Rat	—	170	510	1,190	—	170	170	2,210
Least Shrew	54	—	5	40	13	22	9	143
Total Biomass	10,197	1,292	2,088	4,013	1,400	4,809	1,152	24,951
Number Individuals	290	118	126	262	139	822	299	2,056
Biomass/No. Individuals	35.2	10.9	16.6	15.3	10.1	5.8	3.8	12.1

from the pellet analysis showed the lowest biomass of rodents during the winter and spring of 1971 (Tables 10 and 11).

Predator-prey relationships.—The Barn Owl population on the Welder Refuge seemed well adjusted to the carrying capacity of the area, and did not change greatly until the crash of all small mammal populations in 1970. Prior to 1970, some individual prey species occurred at high population levels while others were low. However, the overall prey population of mammals during the Barn Owl breeding seasons appeared sufficient to meet the requirements of the owls. The total owl population maintained a constant rate of food consumption during years preceeding the 1970 rodent crash. A year-to-year increase in Barn Owls was not apparent because of the balance between the predator and prey populations. Thereafter, however, a decline in the total owl population was preceeded by a decline in the populations of rodents.

Thus the increase or decrease in any one small mammal population appeared to have had no immediate effect on Barn Owl nesting density or success, but the productivity of the Barn Owl population was greatly reduced when the overall small mammal population decreased in availability to a point where the Barn Owls depended on birds for 32 per cent or more of their food.

SUMMARY

A study of Barn Owl ecology was begun in 1965 at the Welder Wildlife Refuge, Sinton, Texas, and continued to the summer of 1971. Additional study of the small mammal prey populations took place between 1969 and 1971.

The seasonal fluctuations of the rodent populations were severe, and trap success ranged from 48.3 to 1.9. Blackbird populations varied between an estimated 50,000 birds during the winter to 15,000 in the spring and summer. The availability of blackbirds as owl food was not limited.

Food habits of the Barn Owl were determined from pellet analysis. This material contained 11,408 food items of which mammals comprised 85 per cent, birds 13 per cent, and insects 2 per cent. A strong correlation existed between the percentage frequency and the percentage biomass of these foods.

Barn Owls initiated their nests in the first three months of the year with a peak of activity in March. The nesting season was irregular, lasting from two to ten months. Clutch size was calculated as 4.9 eggs per nest. Nesting success over a 7-year period was 65.9 per cent.

There were 1.5 times as many young raised per pair in years when rodent prey populations were abundant than in years when prey was less available.

Both the quantitative and qualitative nature of Barn Owl foods are important as the otherwise abundant blackbird population did not sustain successful Barn Owl breeding as measured by fledged owlets per pair. The changes occurring in a single small mammal population had no immediate effect on Barn Owl nesting density or success. However, when the overall small mammal population decreased in their availability as prey, the productivity of the Barn Owl population was greatly reduced. This point was reached when birds made up at least 32 per cent of the Barn Owl diet. Mammals, rather than birds, were the key staple on which Barn Owl reproduction depended.

ACKNOWLEDGMENTS

We express our gratitude to Marshall White and C. Robert Watts for use of their unpublished data on the food habits of owls from 1965 to 1968. Steven Labuda assisted with inspections of the nest boxes and Ronald Cherry helped with the rodent census. An early draft of the manuscript benefited from the reviews of Robert Packard, Donald Klebenow, and Billie E. Dahl; the final revision was reviewed by M. Kent Rylander.

LITERATURE CITED

- BOLEN, E. G. 1967. Nesting boxes for Black-bellied Tree Ducks. *J. Wildl. Mgmt.*, 31: 794-797.
- BOX, T. W., AND A. D. CHAMRAD. 1966. Plant communities of the Welder Wildlife Refuge. Welder Wildl. Foundation. Contrib. 5, Series B.
- CRAIGHEAD, J. J., AND F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Wildlife Management Institute, Washington, D.C.
- DAVIS, D. E. 1959. Manual for analysis of rodent populations. School of Hygiene and Public Health. The John Hopkins Univ., Baltimore, Maryland.
- ERRINGTON, P. L. 1932. Technique of raptor food habits study. *Condor*, 34:75-86.
- GLADING, B., B. F. TILLOTSON, AND D. M. SELLECK. 1943. Raptor pellets as indicators of food habits. *California Fish and Game*. 29:92-121.
- GLASS, B. P. 1951. A key to the skulls of North American mammals. Oklahoma State Univ., Stillwater.
- HENNY, C. J. 1969. Geographical variation in mortality rates and production requirements of the Barn Owl (*Tyto alba*). *Bird-Banding*, 40:277-290.
- KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecol. Monogr.*, 36:239-273.
- LACK, D. 1947. Significance of clutch size. *Ibis*, 89:302-350.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford.
- REED, C. I., AND B. P. REED. 1928. The mechanism of pellet formation in the Great Horned Owl. *Science*, 68:259-260.
- SOUTHERN, H. H. 1955. Nocturnal animals. *Sci. Amer.*, 193:88-98.
- WALLACE, G. J. 1948. The Barn Owl in Michigan; its distribution, natural history and food habits. *Michigan Agr. Exp. Sta., Tech. Bull. No. 208*.

DEPARTMENT OF RANGE AND WILDLIFE MANAGEMENT, TEXAS TECH UNIVERSITY, LUBBOCK, TEXAS 79409 (OTTENI AND BOLEN) AND WELDER WILDLIFE FOUNDATION, SINTON, TEXAS 78387 (COTTAM). 10 DECEMBER 1971.